

VARIABLE EXPRESSION OF THE APPENDICULAR STATUS OF THE MEGAPHYLL IN EXTANT FERNS WITH PARTICULAR REFERENCE TO THE HYMENOPHYLLACEAE¹

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ABSTRACT

Leaf-branch relationships and certain aspects of leaf ontogeny are described in representatives of 15 of the hymenophyllaceous genera (sens. Copeland). A series is discussed from leaves which are non-appendicular, *i.e.* which are direct continuations of stems, to others which are appendicular, *i.e.* which are bilateral and dorsiventral and different from stem apices from their inception. The results are discussed in a broader context of leaf determination and megaphyll phylogeny in the Filicales.

Any attempt at this point on the writer's part to synthesize or to accept a strict definition of a leaf would artificially limit the overall consideration of the spectrum of organ types which are now recognizable among ferns and fern-like plants as leaves. Much of this range (in form, structure, and ontogeny) now appears to exist among the extant Filicales which is a prime thesis of this presentation.

Stem-like features of certain clearly recognizable filiclean fronds have long been recognized. These are the occasionally radially organized petiolar steles at the bases of fronds (Hymenophyllaceae, Stromatopteridaceae, Psilotaceae), indeterminate growth of fronds (Lygodiaceae), delayed organ determination, *i.e.* retention of dual ontogenetic potentials (Osmundaceae), and presence of a stem-like apical cell in the leaf, at least during early stages of development (Osmundaceae). More recently, stem-like features of the leaf primordia of *Stromatopteris*, *Gleichenia*, and *Actinostachys* have been described (Bierhorst, 1968a, b, 1973) as well as stem-like steles at the bases of petioles in *Gleichenia*. In addition, the frond nature of what has been called "aerial shoot" in *Tmesipteris*, although in part long-known (Sykes, 1908), has recently been brought to attention (Bierhorst, 1968b). Most significantly, the non-appendicular nature of the frond of *Gonocormus* (*Trichomanes*), *Stromatopteris*, *Tmesipteris*, and *Psilotum* has been brought out, along with evidence that fronds of *Gleichenia* and *Actinostachys* may similarly be interpreted (Bierhorst, 1973).

Much of the above information supports the basic conclusion that filiclean fronds are megaphylls, that is phylogenetically derived from branch trusses, and it is generally significant that leaves with characters suggestive of stems all fall within families with an overall preponderance of primitive features.

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There are also strong indications of morphological reversals in the basic trend from stem systems to fronds. The species in the Psilotaceae which was formerly considered to exhibit the most primitive morphology of its family, *Psilotum nudum*, now seems to show the most advanced. A very parallel trend also appears within the genus *Schizaea* in which one undescribed Fijian form (possibly a form of the very polymorphic *S. dichotoma*) exhibits a decussately dicotomous instead of a pinnate frond.

Two features of fern fronds are to be emphasized presently. One is the lack of (or at least long delayed) determination which is so pronounced in the Psilotaceae and Stromatopteridaceae and now appears in the Hymenophyllaceae. The other is the non-appendicular status of fronds now extended to various members of the Hymenophyllaceae and the transition of this status to one which is completely appendicular.

A major purpose in undertaking further studies of the Hymenophyllaceae was to clarify the apparently anomalous morphological status of *Gonocormus* (*Trichomanes*). Several New Caledonian collections of this peculiar "genus" were described (Bierhorst, 1973), and these bore what were obviously non-appendicular fronds. It was tempting to compare *Gonocormus* at the time to genera of other families with suggestively similar features, namely *Psilotum*, *Tmesipteris*, *Stromatopteris*, *Gleichenia*, and *Actinostachys*. Such a comparison, however, did not seem proper until *Gonocormus* was first placed in a proper comparative context within its own family, and hence more parallel information was sought.

MATERIALS AND METHODS

All materials used were fixed in the field in a CRAF solution and later transferred to glycerine-alcohol for storage.

Below are listed the species studied, their source of origin, and collection numbers. PNG = New Guinea, S = Surinam, FG = French Guiana, NC = New Caledonia, F = Fiji.

Hymenophyllum (*Mecodium*)

- H. badium* PNG 147, 153, 166
- H. crispatum* PNG 258
- H. polyanthos* PNG 227
- H. javanicum* PNG 282
- H. longifolium* PNG 171A
- H. sp.* PNG 134

Hymenophyllum (*Amphiterium*)

- H. laminatum* PNG 136A, 179
- H. geluense* PNG 171B
- H. sp.* PNG 371B

Hymenophyllum (*Meringium*)

- H. holochilum* PNG 142
- H. acanthoides* PNG 237, 259, 260, 275, 277, 278, 281, 298, 307
- H. gorgonium* PNG 154, 131
- H. bontocense* PNG 355

Trichomanes (*Macroglena*)

- T. meifolium* PNG 130, 280; NC 573

Trichomanes (*Nesopteris*)

- T. grande* PNG 48, 60, 65, 67, 317
- T. harveyi* F 119

Trichomanes (*Callisopteris*)

- T. apiifolium* PNG 350

Trichomanes (*Crepidopteris*)

- T. gracillimum* PNG 20, 137, 309
- T. humile* PNG 42, 325
- T. alternans* F 126
- T. sp.* PNG 133A

Trichomanes (*Gonocormus*)

- T. sp.* PNG 128, 144, 148, 149, 261, 275, 333

Trichomanes (*Vandenboschia*)

- T. aphlebioides* PNG 45
- T. giganteum* PNG 356

Trichomanes (*Cephalomanes*)

- T. atrovirens* PNG 50, 51, 55, 56, 64, 314, 324, 326, 328
- T. asplenioides* PNG 318, 327
- T. australicum* F 73

Trichomanes (*Microtrichomanes*)

- T. digitatum* PNG 132, 133B, 136B
- T. francii* NC 576

Trichomanes (*Selenodesmium*)*T. obscurum* PNG 90, 95, 96, 112, 177*T. dentatum* F 30; NC 460*T. sp.* PNG 66, 100, 105, 145, 151, 152, 270, 272, 292, 305, 342*Trichomanes* (*Microgonium*)*T. beccarianum* PNG 348*T. motleyi* S 81, 136, 183*Trichomanes* (*Crepidomanes*)*T. venulosum* PNG 61, 194*Trichomanes* (*Didymoglossum*)*T. montanum* S 103, 140, 141*Trichomanes* sens. strict.*T. pinnatum* FG 44, 46*T. sp.* FG 121*Trichomanes* (*Feea*)*T. diversifrons* FG 176

DESCRIPTIONS

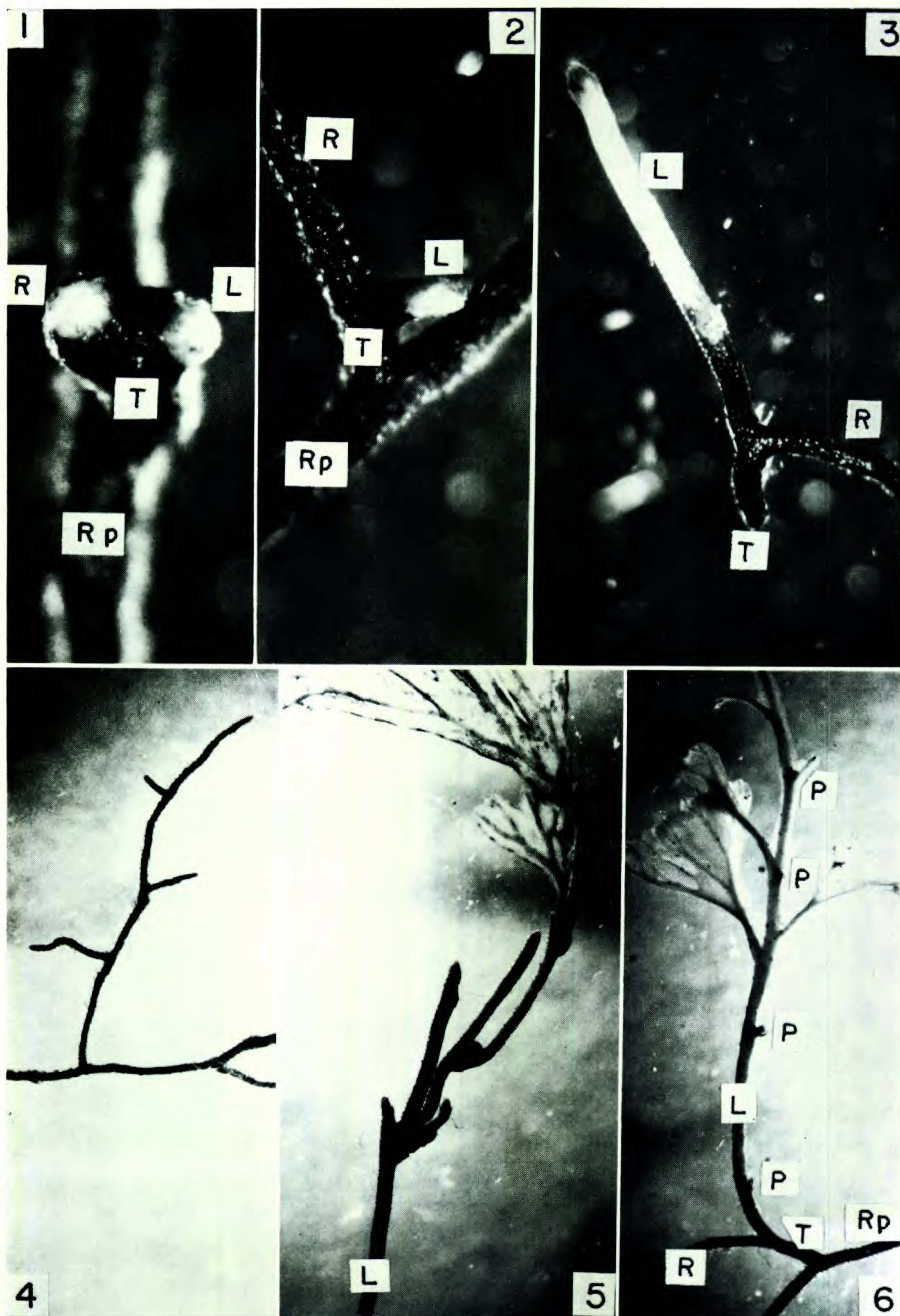
The New Caledonian *Gonocormus* specimens studied showed a rootless body with a system of filamentous, hairy running stems. The runners bore distichously arranged lateral stems which in turn grew as the parental ones. In addition, vertical branches were produced which fell outside of the basic $\frac{1}{2}$ -cladotaxy of the runner system. The vertical branches dichotomized soon after their production, and of the two new apices formed, one became a new runner and one a "leaf." The ambiguity lies in the different designations of what a leaf is in *Gonocormus* (see Copeland, 1933). The apex which forms the "leaf" branches apically in a plane at right angles to the stem dichotomy below, and of the two new apices formed, in some collections the one on the abaxial side with respect to the original parental runner forms blade after its radially symmetrical apex assumes a linear form. The sister apex on the adaxial side branches as did its mother apex, and the process of branching and blade formation may continue until 5 or 6 blades with their planes more or less parallel to each other are produced. A leaf of this type, from which three blades have been removed, is illustrated for a New Guinea collection in Figure 5, the axes extending vertically in the photograph. In the less flabellate and more pinnate leaves, the leaf apex frequently drops off a series of these "proliferation" apices (P, Fig. 6) which may or may not produce new blades or whole "leaves."

The species designation in this context is not possible at present. According to Copeland (1933) there may be only one species or 5 or more of *Gonocormus*. Extreme variability and overlap in size and leaf form have not, and cannot be here, reconciled in a satisfactory system designating specific circumscriptions.

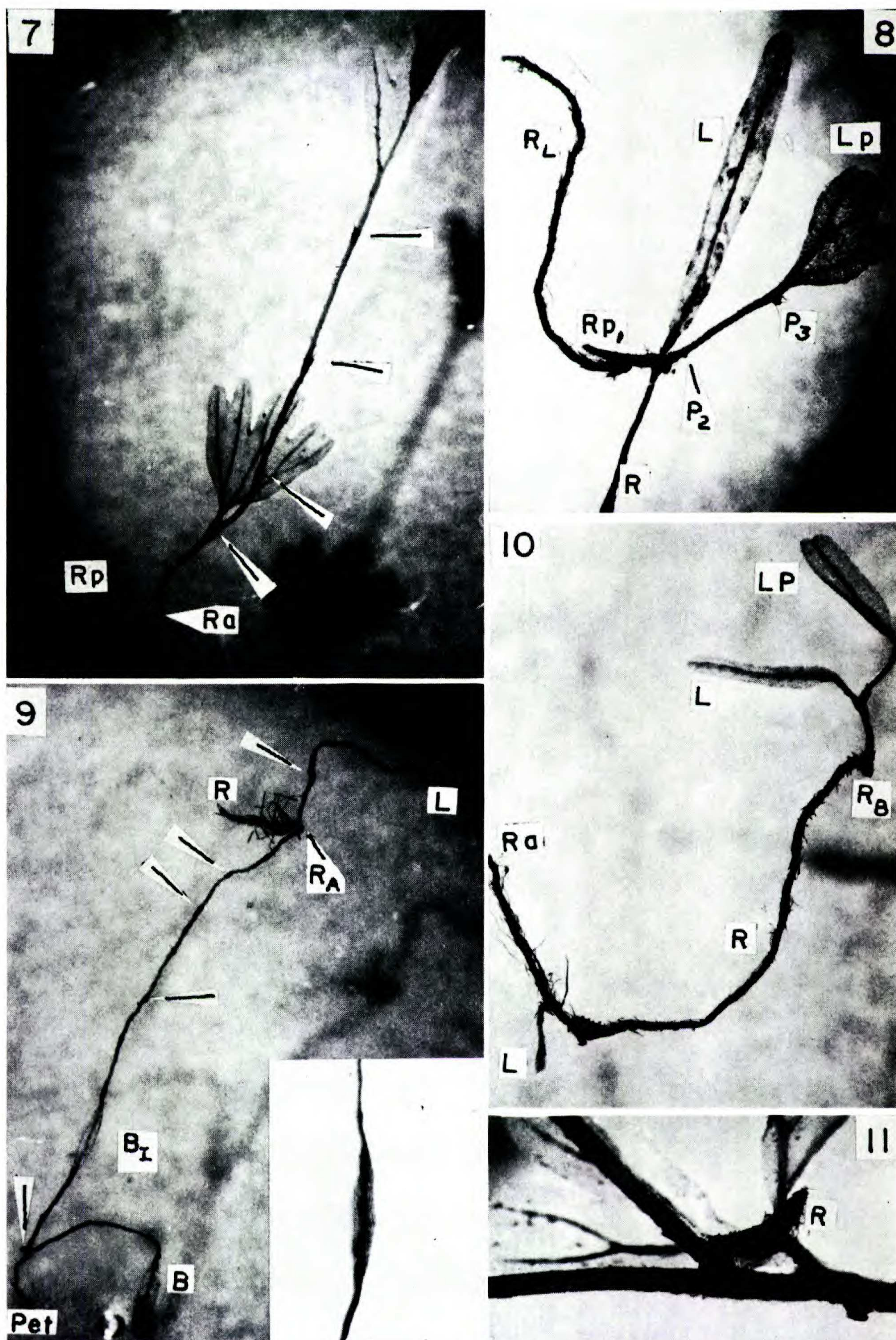
New Guinea collections, numbering 9 being described, varied considerably among themselves, but all differed in one particular way from the New Caledonian ones. In the New Guinea ones, the branches which formed leaves were not on the upper side of a runner, but all fell within the $\frac{1}{2}$ -cladotaxy of the laterally placed stems. After this was observed, more of the original New Caledonian material was examined, and in a few cases the leaf-bearing branch was also to be lateral.

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FIGURES 1-6. *Trichomanes* (*Gonocormus*).—1-3. Successively older stages in the development of the phylliferous lateral stem. 1-2, PNG 128, $\times 21$; 3, PNG 144, $\times 18$.—4. A runner stem, horizontally oriented, bearing two laterals; the upper one again bearing alternate runners. PNG 275, $\times 4.8$.—5. One leaf several times compounded by "proliferations." Three blades



have been removed. PNG 144, $\times 7$.—6. A portion of the runner, Rp, bearing a branch, T, which has bifurcated to produce runner, R, and leaf, L. P indicates "proliferation" apices which have not grown out. PNG 149, $\times 7$.—Rp = parental runner; T = trunk of a leaf-bearing branch; R = runner; L = leaf.



FIGURES 7-11. *Trichomanes* (*Gonocormus*).—7. An entire fertile leaf and its apparent attachment to the parental runner, Rp. Ra is the apex of the runner which forms the second

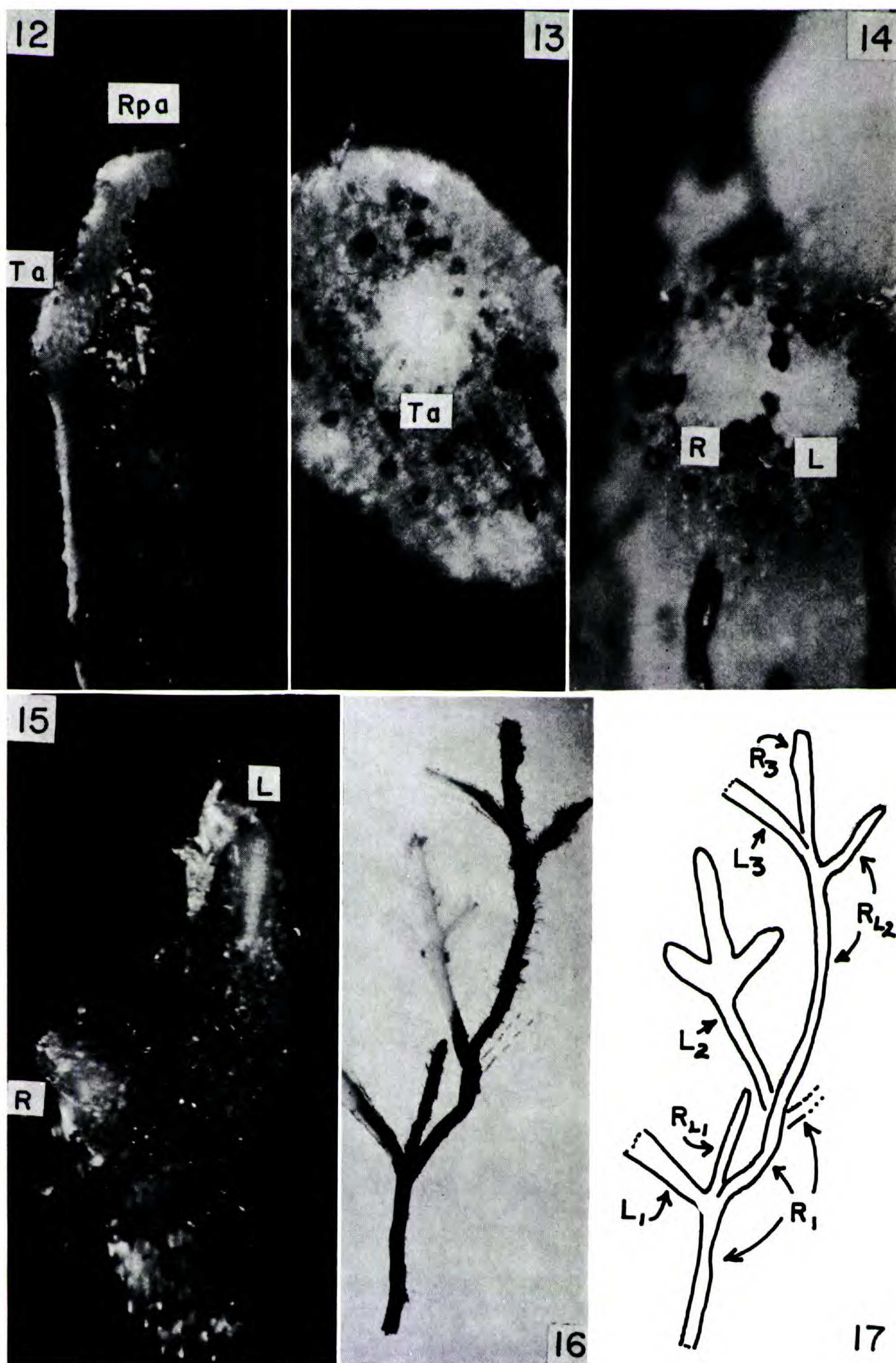
The formation of lateral branches on a runner is quite regular. Although on branching two apices of equal size are formed, one remains medianly situated at the apex of the runner (illustrated for *Crepidomanes*, = *Trichomanes* sens. lat., which shows identical branching, Fig. 12). The lateral apex branches in the vertical plane (Fig. 1) to produce two identical apices. The upper of these then forms "leaf," while the lower forms a new runner (Fig. 2, 3, 6). Or one or both of the two apices may remain dormant (Fig. 7, Ra). In the specimen shown in Figure 4, a branch runner is shown oriented vertically in the photograph, which again shows alternate, 2-ranked runner branches. At all but one point of branching, a dormant apex was seen at the base on the upper side. In a very few instances a lateral branch such as the one shown in Figure 1 formed two new runners rather than one runner and one leaf.

A further deviation from the pattern described above was found in one of the New Guinea collections in which proliferation apices well up on a "leaf" grew into new runners (Fig. 11) instead of new blades. In the same collection, new runners were observed arising from single cells on the lower sides of veins of old partly decayed laminae.

The most peculiar and most diminutive *Gonocormus* collection was PNG 171, also from New Guinea (Fig. 7-10, note magnifications) in which the broadest lamina (lower one on the fertile "leaf," Fig. 7) was approximately 3 mm across with most others in the range of 0.5-1 mm and in which the runners were mostly between 90 and 170 μ in diameter! Much of the morphology of PNG 171 was similar to that of other collections. That is, a runner branched laterally, and lateral branches performed as described and illustrated in Figures 1-3. In Figure 7, Rp is a parental runner bearing a lateral branch. The branch dichotomized. An arrested apex was left behind (Ra), while its sister apex formed the "leaf." The broader blade at the base formed first. The first proliferation apex continued upward, leaving behind 4 arrested proliferation apices (at pointers) then formed the upper blade with the sorus. In Figure 10, a runner, R, with its older end broken off at R_B, produced blade L and a blade LP from its first proliferation. Runner R also produced two more lateral branches, one of which produced another leaf, L at lower right, and the other which is just below the runner apex Ra and too small to be indicated. Also in PNG 171,

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member of the bifurcation of the short branch which bears the leaf. Four "proliferation" apices are pointed out. $\times 6.1$.—8. A unit such as shown in Fig. 1-3 and 6, but terminal on a runner, R, rather than lateral. L = first blade; L_p = blade of first proliferation; P₂ and P₃ = second and third proliferations upon the first; Rpl = a runner from the first proliferation which bore a lateral runner, R_L. $\times 8$.—9. What began as a "leaf." Pet is its petiole; B = first lamina. Lower pointer indicates the apex of the first proliferation of the first proliferation of the original "leaf." B_i is an intercallary blade, enlarged in inset, produced by the first proliferation before it went on to form runner with lateral apices, pointers. The apex of the runner was broken off at R_A. It had produced a lateral truss (equivalent to the one in Fig. 3); R = its runner, L = its leaf. $\times 8$.—10. A runner, broken off at R_B, produced a lateral truss (L = its first blade; L_p blade from its first proliferation) and another one, L. Ra = runner apex. $\times 8$.—11. A runner, R, arising from a proliferation well up upon a frond whose major axis lies horizontally in the figure. $\times 9.6$.—7-10, PNG 171; 11, PNG 275.



FIGURES 12-17. *Trichomanes* (*Crepidomanes*) *venulosum*.—12. A runner tip, Rpa, and a lateral truss primordium, Ta. PNG 61, $\times 100$.—13. Face view of truss primordium. PNG

the phylliferous unit (as illustrated in Fig. 3 for another collection) was occasionally terminal rather than lateral upon a runner (Fig. 8). In the figure, blade L was the first formed lamina; Lp is the blade of the first proliferation. The apex of the first proliferation before producing blade Lp produced three other proliferation apices; the second and third, P₂ and P₃, remained arrested. The first, however, formed a runner, Rp₁, which in turn produced a lateral runner, R₂.

Another peculiarity of PNG 171 was its ability to change a lamina apex back into a runner apex. The specimen in Figure 9 is what began as a "leaf" (Pet designates the petiole which forms the trunk of the truss). The blade B formed first. The first proliferation apex formed the rest of the specimen. It dropped off a proliferation apex (lower pointer), formed a lamina, B₁ (enlarged in inset), and grew on while leaving behind three more proliferation apices (next 3 pointers). It, now acting as a runner apex, produced a lateral branch (again of the usual *Gonocormus* type as shown in Fig. 3) before the apex became arrested (R_A). The lateral branch forked to produce runner R and leaf L with one proliferation apex (upper pointer).

Among the other Hymenophyllaceae studied, *Crepidomanes*, *Microgonium*, and *Didymoglossum* (all three = *Trichomanes* sens. lat.) were most similar to *Gonocormus* in that they are rootless and possess thin running stems which branch alternately in the horizontal plane, although in *Microgonium* the arrangement is less regular and frequently seems to approach helical.

Crepidomanes is illustrated in Figures 12–17. A runner apex, Rpa in Fig. 12, and a lateral branch apex, Ta (also shown in face view in Fig. 13), are shown. The equivalent of the trunk of the phylliferous branch of *Gonocormus*, i.e. T in Figs. 1–3 and 6, is almost non-existent as the apex Ta bifurcates earlier (Fig. 14). This is also true of *Microgonium* and *Didymoglossum*. The leaf apex L may be designated as such only due to its position, since the dichotomy is always in the vertical plane and the upper of the two apices regularly forms leaf while the lower forms a new runner. A somewhat later stage appears in Figure 15, where the leaf apex now has developed a linear form and the prismatic layer is readily visible.

At maturity the system appears as in Figure 16 with an explanatory diagram in Figure 17. Runner R₁, which is broken off at dotted lines, produced lateral branch 1, which bifurcated to form leaf L₁ and runner R_{L1}. R₁ also produced lateral branch 2, which similarly bifurcated to form leaf L₂ and runner R_{L2}. R_{L2} continued growth and produced branch 3.

In *Crepidomanes* the lateral branches of the smallest runners generally

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194, × 130.—14. A lateral truss has bifurcated to form a runner apex, R, and a leaf, L. PNG 194, × 130.—15. An older stage than in Fig. 14. The leaf L now shows a linear apical meristem. PNG 61, × 95.—16. A runner with lateral trusses. PNG 61, × 6.25.—17. Explanatory diagram for Fig. 16. The runner, R₁ which is broken off at dotted lines, produced truss 1 which bifurcated to form leaf L₁ and runner R_{L1}. Truss 2 was next produced by R₁ which next produced leaf L₂ and runner R_{L2} which in turn produced truss 3 with its leaf L₃ and runner R₃.

produce no leaves. They frequently, however, leave behind at their point of attachment an arrested apex on their upper side.

In mature portions of *Didymoglossum* and *Microgonium* the runner apex which is formed by the bifurcation of a lateral branch is most often non-functional, but by careful dissection it can be seen as a minute area of white tissue, 4 or 5 cells across, completely hidden by hairs on the upper side of and at the base of what appears to be petiole.

Microtrichomanes (= *Trichomanes* sens. lat.) like the other "genera" described above has a very thin runner with a series of lateral branches. The branches, however, are arranged spirally to irregularly, and the plant bears roots which, like all hymenophyllaceous roots, are endogenous in origin. Externally the roots are quite difficult to distinguish from running stems since they are of similar size, bear similar hairs, and the calyptra is very diminutive.

Lateral branches in *Microtrichomanes* originate much as do those of *Crepidomanes* and others described above. They grow out from the runner each as a short, broad cone rather than a cylinder, and they bifurcate. The plane of bifurcation is at right angles to that in *Gonocormus*, *Crepidomanes*, *et al.* and therefore produces one apex toward the tip of the runner and one away, rather than one on the upper and one on the lower side. Of these new apices, the one away from the runner apex forms leaf after its radial symmetry shifts to bilateral symmetry. Very shortly after the bifurcation, the leaf apex is also slightly larger than its sister apex which may remain dormant, grow out as a new runner, or bifurcate to produce a second leaf and another apex which also has variable potential.

The "genera" *Crepidopteris* (= *Trichomanes* sens. lat.), *Amphiterium*, *Meringium*, and *Mecodium* (all three = *Hymenophyllum* sens. lat.) and morphologically very similar to each other in terms of those characteristics considered in the present context. Each bears easily recognizable roots, and a running stem with lateral branches in a fixed cladotaxy which is spiral in *Amphiterium* and spiral to irregular in *Mecodium* and *Crepidopteris*. In *Meringium* the arrangement is 2-ranked with the two rows somewhat above the lateral position and therefore separated from each other by less than 180°.

The lateral branches of these four "genera" branch in the same plane as do those in *Microtrichomanes*, and of the two new apices formed the abaxial one usually forms leaf and adaxial one remains stem which may grow out as a new runner or more often remain dormant. Several times in *Amphiterium* and *Meringium* the apex in the leaf position has been seen to form a new runner instead of a leaf, and in these cases its sister apex in its apparent axil remained dormant. In one case both apices formed runners. In addition, the bud in the apparent axillary position occasionally bifurcated again to produce another leaf and another stem apex. In each of these four genera, as in others described, the young leaf apex is very similar in form and structure to the stem apices of the rest of the body until bilaterality sets in.

A still more significant variation observed in *Amphiterium* and *Meringium* is the occasional transformation of the tip of a long runner directly into a leaf.

Macroglena (= *Trichomanes* sens. lat.) shows also a creeping stem, but it is not so thin. It bears spirally arranged appendages which superficially appear to be leaves with near axillary buds. The manner in which these appendages originate and the parallelisms with other hymenophyllaceous "genera" allow these to be designated as branches of the stem. *Macroglena* bears prominent single apical cells on all of its apices, and the primordia are relatively large. This allowed for more detailed ontogenetic analysis down to the cell-lineage level than was possible for genera with minute apices without apical cells such as *Gonocormus* and *Microgonium*.

The apex of a runner in *Macroglena* possesses an apical cell with three cutting faces. An equal division of the apical cell initiates a new runner apex and the apex of a phylliferous branch (what has been called a leaf). When the two apices are separated by approximately 6–8 cells, their form is still identical, but one may be designated as the future leaf-producing structure (L in Fig. 18) by its position in the cladotaxy (formerly called phyllotaxy) and the other as runner apex (S).

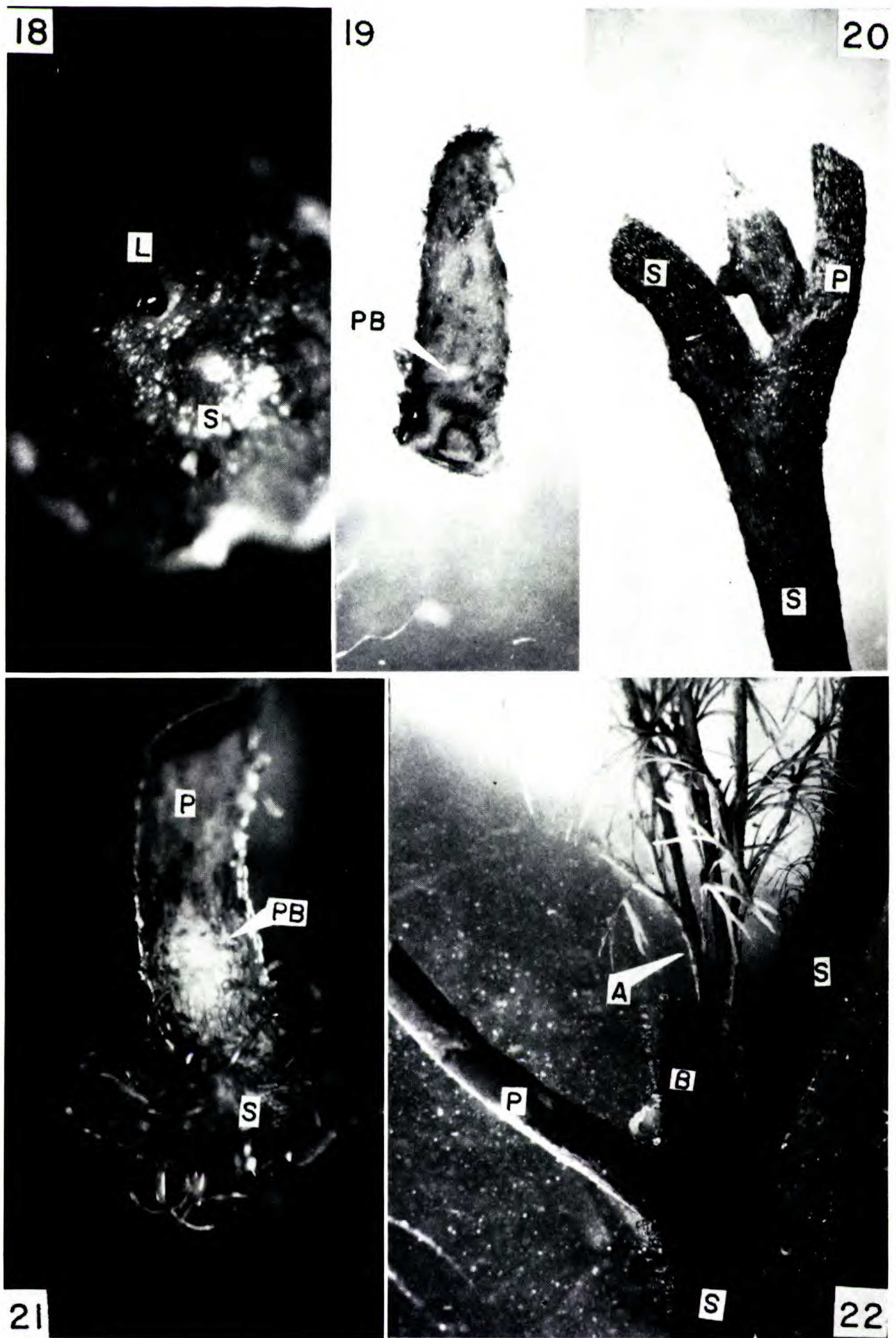
At about this stage, the shape of the future leaf-producing structure changes slightly; it becomes slightly longer in the direction at right angles to the line between it and its sister apex (the new runner apex). The apical cell is still triangular in top view, but one linear prismatic series of cells emanates from it down one of the narrow sides and two down the other. Soon thereafter a single, curved division wall of the apical cell cuts off one of its corners and establishes one cutting face where there were two, and the bilateral apical cell is oriented with its long axis (as viewed from above) directed toward the apex of the running stem.

It is close to this stage when the apex of the future phylliferous structure divides to leave behind an apex on its adaxial side. One such apex is shown situated on the adaxial side of what appears to be petiole of a young leaf in Figure 19 (PB) and on a slightly older structure in Figure 21. In the specimen shown in Figure 20 the seeming epipetiole bud has grown out and also has produced one root.

The "epipetiole" bud in *Macroglena*, according to its ontogeny and also by extrapolation of parallel information from other hymenophyllaceous forms, is then considered to be the sister apex of the leaf apex with both structures borne at the tip of a short lateral branch.

The "genera" *Cephalomanes*, *Selenodesmium*, *Nesopteris*, *Calliopteris*, *Trichomanes* (sens. strict.), and *Feea* (all = *Trichomanes* sens. lat.) have similar leaf-branch relationships. They each have relatively stout upright to tilted stems bearing closely crowded foliar appendages in a spiral order (divergence ca. 120°). They all bear roots and what are seemingly axillary, or near-axillary, buds.

In these forms the stem steles are radially organized protosteles. The trace to what has been called a leaf is similar, and from it the bud trace arises. Petiole strands become more dorsiventral and therefore more leaf-like in the traditional sense farther up. In those "genera" with thin, creeping stems the information is not comparable. Very delicate forms often have only 1–3 tracheids



FIGURES 18-22.—18-21. *Trichomanes* (*Macroglena*) *meifolium*.—18. The stem apex bifurcated to form a “leaf,” L, and a new stem apex, S. $\times 83$.—19. An entire leaf bearing

in the stele. Larger creeping forms mostly show dorsiventral steles throughout their axial systems (see Bower, 1926).

Trichomanes sens. strict. is illustrated in Figures 23–25. One entire plant stock with petioles, roots and hairs removed appears in Figure 23. The axis was overtopped twice (aborted apices at SA) by lateral apices. BP indicates a lateral branch which grew out and later aborted. The tip of the specimen in Figure 23 is shown enlarged in Figure 24. A comparable photograph of another species appears as Figure 25 in which BP designates the lateral buds which are clearly not axillary.

The origin of the buds which appear epipetiolar was observed in *Trichomanes* sens. strict. and in *Feea*. They originate from the leaf apex just as they do in *Macroglena* and just as do the “proliferation” apices in *Gonocormus*. In fact, the same kind of bud origin has been described in *Psilotum*, *Stromatopteris*, *Gleichenia*, and *Actinostachys* (Bierhorst, 1968b, 1973).

Buds in similar positions occur in dennstaedtioid genera, but they have been described as originating on the stem (Bierhorst, 1973) and not from the leaf apex. In conjunction with the present studies, several grammitid genera were examined in which buds appear on the sides of the petioles near the base. These also were of stem origin and therefore not comparable.

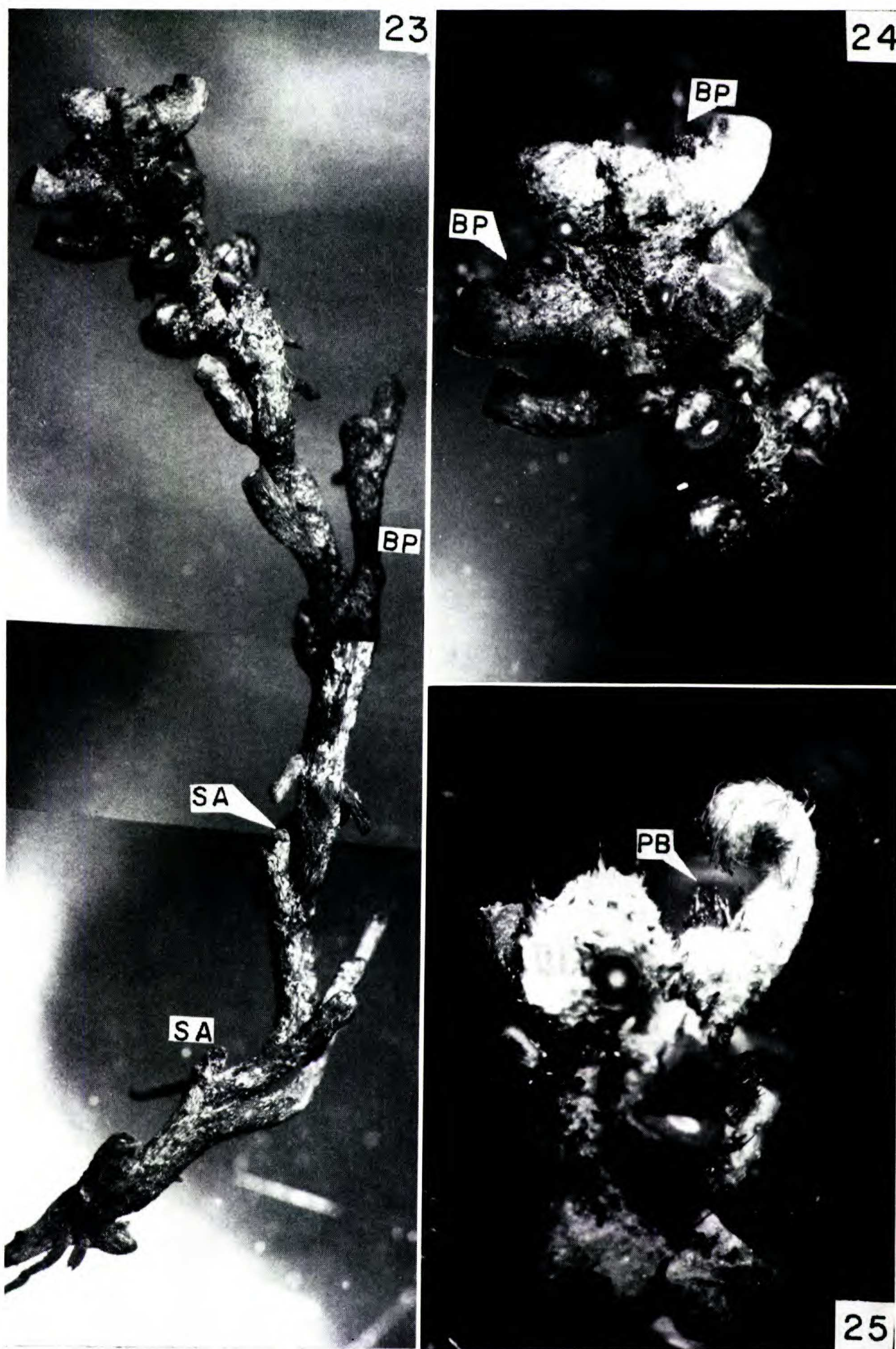
Vandenboschia (*Trichomanes*) *aphlebioides* differed from the other hymenophyllaceous forms studied. The species has a relatively stout stem which creeps upward on tree trunks. Leaves are borne in subopposite pairs, but leaves of successive pairs are not within the same orthostichy, and the phyllotaxy approaches spirodistichous. In the axil of each leaf (Fig. 22) or commonly above the axil on the stem (S) is a bud (B). Toward the stem on the bud, but slightly out of direct alignment between the stem and the center of the bud, is the aphlebia (A) which has a linear attachment to the bud and is branched in a fan-like manner.

The leaf apex appears much like that of *Macroglena* at an early stage in development. Its apical cell has three cutting faces when young, but soon after the primordium is recognizable as a distinct bump, the apical cell has two cutting faces. The leaf primordium soon comes to be situated down the side of the domeshaped stem apex, but growth of the stem tissue below pushes the primordium upward and changes its orientation so that it becomes reoriented forward and falls on the broad flat end of the stem tip. The bud originates above the leaf primordium on the stem and therefore does not seem to have the same origin as buds in seemingly comparable positions in other hymenophyllaceous forms.

On the flat, distal face of the bud, several cells toward the parental stem from the apical cell of the bud, a single line of cells bulge, divide, and act as a

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a petiolar apex, PB. $\times 13.5$.—20. A stem, S, bearing a “petiole,” P, with a bud. The bud has produced one root. $\times 10$.—21. A stem, S, bearing a petiole, P, upon which is a bud, PB. $\times 21$.—22. *Trichomanes* (*Vandenboschia*) *aphlebioides*. Stem, S, bears branch, B, which produced a leaf, P = its petiole, and an aphlebia, A. $\times 3.3$.



FIGURES 23-25.—23. *Trichomanes* (sens. strict.) sp. Entire stock of one old plant. The apex of the near-vertical stem aborted twice at SA and was overtopped in each case by a lateral

linear meristem. The meristem, oriented circumferentially on the bud, soon divides itself to establish the branches of the aphlebia. This kind of origin would be quite unique among all fern leaves, if the aphlebiae were to be called leaves. Interpretation of aphlebiae in this case requires further information.

The buds of *Vandenboschia aphlebioides* occasionally grow as new running stems, but generally they remain dormant. They produce one or two leaves which originate in a manner similar to those on the runners. Leaves on lateral buds, however, mostly remain arrested in the primordial stage.

Another species of *Vandenboschia* studied was a terrestrial plant with more tufted leaves and without aphlebiae. The stem was essentially short-creeping. Phyllotaxy was similar but less regular and seemed to approach spiral. Buds were distinctly epipetiolar, but insufficient material was available to determine their origin.

DISCUSSION AND CONCLUSIONS

In discussions of the phylogeny of megaphylls, the following morphological changes are generally enumerated: overtopping, planation, and webbing. These are sufficient to characterize a sequence of mature forms in the general way, but webbing must be referred to the origin of a marginal meristem and the sequence of ontogenies involved in overtopping must be considered. In addition, the order of events, their degree of concomitance and their degree of fixation (therefore their capacity to revert) must be argued *separately* for the various megaphyllous taxa.

When overtopping has reached its ultimate, the overtopped branch truss has been reduced to appendicular status at its very inception. This end point has been reached in all extant seed plants and many ferns in which a leaf primordium is totally distinct from the stem apex upon which it is borne. It is dorsiventral from its inception. Evidence from plants with such leaves has been responsible for the interpretation (Wardlaw's concept) that the fundamental leaf features, *i.e.* the external and histological dorsiventrality, are causally related to the initial subordination of the leaf primordium (or its presumptive site) to the stem apex and/or the relative positions of the two. The suggestion of Steeves (1963), based in part on Kuenert's work and more recently supported by differences in the protein spectrum between leaf primordia and stem apices and by changes in the spectrum with increasing age of leaf primordia (Caponetti *et al.*, 1972), that specific leaf-determining substances accumulate in a primordium to the point where one of its ontogenetic options is lost is not necessarily in contradiction to the above interpretation.

Those ferns which bear non-appendicular fronds, *i.e.* those which are direct continuations of stems, certainly contradict Wardlaw's concept. If the concept were broadened by suggesting that a primordium developed into a leaf as a

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branch. FG 121, $\times 3$.—24. Tip of the specimen in Fig. 23. BP = petiolar bud. $\times 5.6$.—25. *Trichomanes* (sens. strict.) *pinnatum*, stem tip. PB = petiolar bud on young leaf. FG 44, $\times 9.8$.

consequence of its position relative to all other components of the plant body (without specifying any particular geometry such as that exhibited by *Dryopteris aristata* and other species like it), then the scope of the concept, however vague, would embrace the non-appendicular fronds of the Hymenophyllaceae and the Gleicheniaceae, since their geometrical relationships are quite fixed. On the other hand, the irregular, or apparently irregular, interrelationships among parts of the somata in the Psilotaceae and Stromatopteridaceae might seem to contradict.

At this point, it might be desirable to entertain Steeves' suggestion in a context divorced from geometrical considerations. But even then, there remain at least two genera, *Psilotum* and *Gonocormus*, in which leaf determination is never complete and in which the frond apex can cease to produce frond and proceed to produce typical stem.

If specific leaf-determining substances do exist, there are clues as to their possible nature. In a number of primitive ferns in which a leaf primordium is very difficult to distinguish from a stem apex, *i.e.* the Psilotaceae, Stromatopteridaceae, *Actinostachys* (young plants only), and various Hymenophyllaceae, the first indication of the selection of the leaf development pathway is the presence of a distinct region of cell elongation below the now-recognizable leaf apex. In the Stromatopteridaceae, *Actinostachys*, and the Hymenophyllaceae, this occurs before differential growth initiates the circinate coil and may precede the transition from an apical cell with three cutting faces to one with two. Into this is read the possibility that substances involved in cell elongation, auxin and/or gibberlins, may be involved in leaf determination in ferns. If indeed cell elongation factors are involved, they may be of either primary or secondary significance with respect to the protein spectrum changes as described by Caponetti *et al.* in *Osmunda*.

As for those morphological changes involved during the phylogeny of the filiclean frond, the following interpretations are presented. This basically represents a further refinement of the theory of double megaphyll phylogeny as presented by Bierhorst (1971, 1973) so as to embrace new information on the Hymenophyllaceae. Although changes are postulated in a definite sequence, it must be allowed (and expected) that during the phylogenetic history of forms which led up to the extant Filicales the changes were occasionally somewhat out of sequence and all changes were to some extent concomitant. It must also be assumed that, although the longtime trend postulated is unidirectional, there were frequent reversals to somewhat more primitive morphology as has certainly taken place in some extant taxa.

The morphological starting point in this theory is a plant with creeping and upright stems, exhibiting dichotomous branching, but not necessarily symmetrical. Ultimate upright axes were eventually determinate, *i.e.* ceased to grow with mature tissue replacing meristematic tissue. Certain ultimate axes became determinate before others, and their positions were irregular throughout the upright truss. It is assumed before determination that all apical meristems throughout the soma had the same developmental potential. In other words, any apex in the horizontal system could grow into an aerial axis, a lower branch of an aerial

axis if close to the substratum could grow into a horizontal stem, or an apex high in the aerial system if accidentally buried could revert to a horizontal stem. It is also assumed that all dichotomies were not necessarily equal at their inception. The starting point conforms in general to a rhyniophyte, although, of course, attribution of developmental potentials of apical meristems represents an extrapolation of information from extant ferns.

It is postulated that lamina formation began very early from plants such as the indicated starting point. Such an increase in photosynthetic surface has occurred in all vascular plant lines and in the same manner: by the introduction of a linear meristem. In ferns and fern-like plants and, in particular, in the Filicales, linear meristems of leaves are derived ontogenetically by modifications of radially symmetrical apical meristems. It is assumed that linear meristems which produced some laminar tissue appeared at the tips of ultimate units in a dichotomous truss before (or along with) any other major morphological (phylogenetic) changes occurred and at a relatively late stage in ontogeny before determination.

(The tendency of ultimate determination of branch units as well as linear meristem formation may well have preceded vascular plant origin and therefore represent ancestral algal characters.)

In that line which led ultimately to the Filicales planation is interpreted to have begun in some of the minor branch trusses of an aerial or more or less upright system, at first better expressed near distal ends and later (phylogenetically) more proximally. The orientation of the planated trusses must have been coplanar throughout an entire upright aerial branch system.

Linear meristem activity is interpreted to have been expressed progressively earlier in the ontogeny of subtrusses of the major aerial systems. When this is expressed before a final division of an apical meristem, as in the extant ferns, the result is webbing of ultimate units and establishment of multiveined ultimate laminar units.

A monopodium with pinnate branching (at first a pseudomonopodium or dichopodium) is assumed to have been established early within the major aerial truss which now might be called a pre-frond. Among extant Filicales pinnate branching and dichotomous branching completely intergrade, and therefore the feature at least in many genera is not yet fixed. The entire sequence of ontogenetic intermediates exists in two genera, *Schizaea* and *Gleichenia*, and the author suspects *Lygodium*. In *Gleichenia* the series seems to be best read from pinnate to dichotomous and is expressed in the first one or two ramifications of the frond. Clearly pseudodichotomous (= pinnate) branching occurs where the frond apex ceases to grow and is overtopped by two pinnae from below. In this case there is a clear remnant of the frond apex with or without several arrested pinnae in the fork of the seeming dichotomy. In other cases in *Gleichenia*, however, the overtopping pinnae are much more precocious, and a series could be shown in which they develop closer and closer to the apex of the frond. The end point is a true ontogenetic dichotomy.

In *Schizaea dichotoma* the leaf at maturity appears equally dichotomous. Ontogenetically, however, a complete series exists between dichotomy and

clearly lateral branching. Apical cells of new frond branches originate as sister cells of other apical cells (= true ontogenetic dichotomy) or from one to 7 cell generations removed from another apical cell.

In the apparently equally dichotomous frond ("aerial shoot") of *Psilotum nudum*, the lower set of bifurcations are pseudodichotomies of the *Gleichenia* type in which the new apical cells arise lateral to another apical cell which ceases to function. In the ontogeny of the more distal "dichotomies" of *P. nudum*, the apex of the trunk below continues while the second limb of an apparent dichotomy develops from a lateral primordium (Roth, 1963).

It can be postulated that cladotaxy, *i.e.* the fixed arrangement of prepinnae upon a prerachis (or prepinnules upon a prerachule as the order of branching dictates), occurred early in the phylogenetic history of the Filicales and that this branching character was also expressed in the insertions of prefronds upon running stems and even running stems upon running stems but in no case to the exclusion of equal apical branching. In various lines within the Filicales, then, one or another branching pattern may predominate or be exclusively expressed. The major reason for extending the branching trend to the entire soma rather than restricting it to prefronds lies in the fact that this is essentially the state which exists in most of the extant, primitive Filicales. If, however, one adheres to Bower's interpretation that an upright stem with spiral phyllotaxy is primitive within the Filicales then there is an apparent contradiction. Bower's interpretation, however, stems from another interpretation that the Osmundaceae forms the main phylogenetic trunk of the Filicales, but since his ideas were published much new information has been assembled all indicating that the Osmundaceae essentially stand alone and may well have been independently derived from all other Filicales.

The phylogenetic process of megaphyllization (planation plus webbing) is assumed to have worked its way from the more distal minor trusses of an aerial stem system toward the major trunks of the system and progressed toward the horizontal stem. Or in other words, modifications in meristems are assumed to have taken place earlier and earlier in the ontogeny of the prefrond. The first foliarized units of the prefrond were then the pinnae, and they are considered megaphylls of one order.

The entire frond (or prefrond) at this point has not evolved to the state of the leaf in any strict definition which one would like to impose. This is essentially the state at which it still exists in several extant filicalean genera. Such a frond arises directly from an apex which has stem-like organization, *e.g.* *Psilotum*, *Tmesipteris*, *Stromatopteris*, *Gleichenia*, *Actinostachys*, *Osmunda*, and a number of Hymenophyllaceae. This apex may be lateral in position, falling within a more or less fixed cladotaxy, *e.g.* *Stromatopteris* (young plants only), *Gleichenia*, *Actinostachys*, and Hymenophyllaceae, or it may be terminal on a longer creeping stem, *e.g.* *Psilotum*, *Tmesipteris*, and several Hymenophyllaceae. The stem or stem-like apex which develops into the frond may do so directly or it may dichotomize one or more times to leave behind apices with various developmental potentials before it finally commits itself to a frond developmental pathway. The final dichotomy of the phylliferous branch apex or frond apex

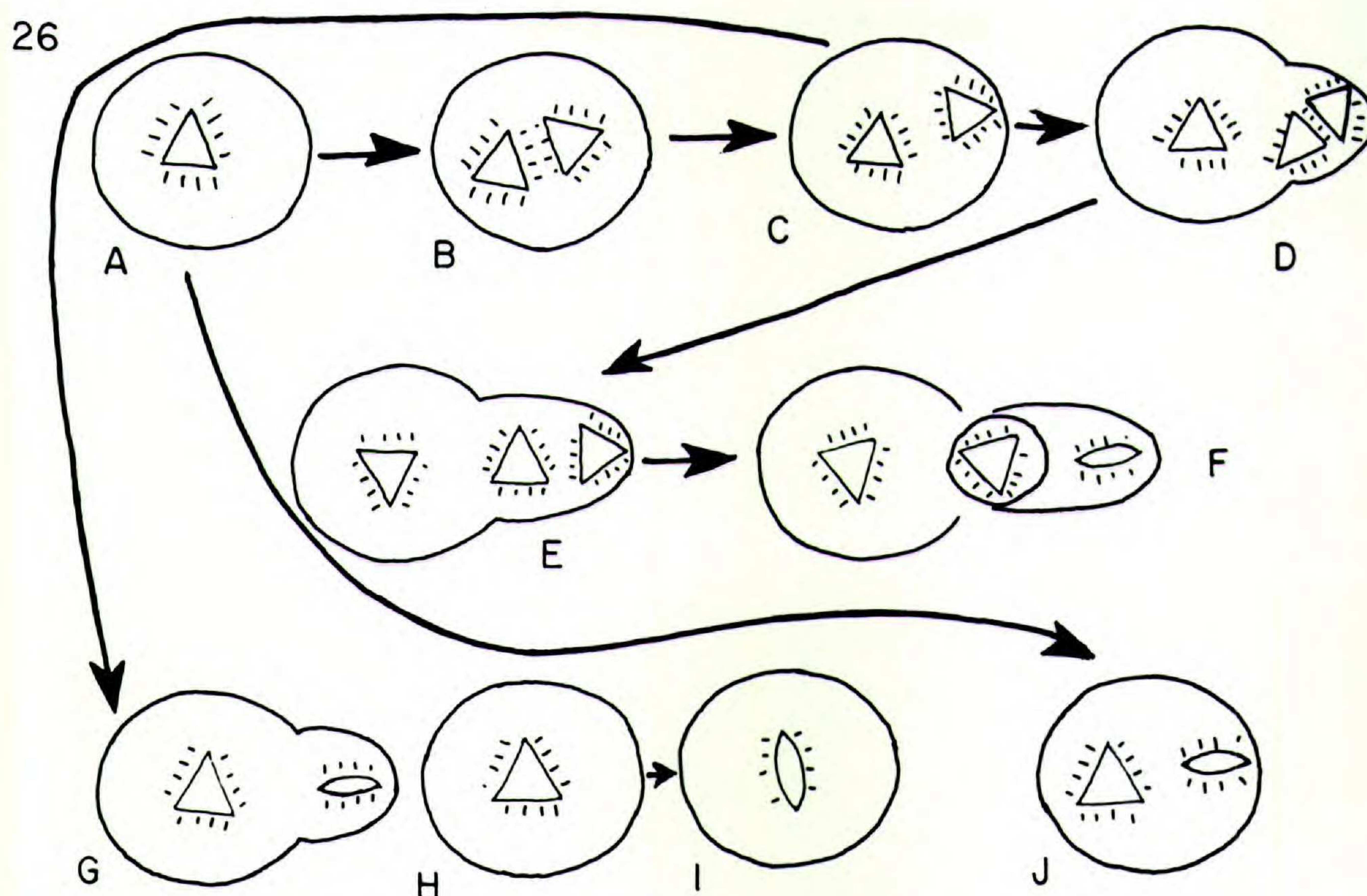


FIGURE 26. Diagrams showing certain aspects of frond ontogeny in various ferns. Explanation in text.

(the designation here is subjective) may result in a bud which is pseudoaxillary (*Stromatopteris*, *Gleichenia*, some Hymenophyllaceae) or apparently quite epipetiolar (*Actinostachys*, *Psilotum*, *Stromatopteris*, some Hymenophyllaceae). In at least two genera, *Psilotum* and *Gonocormus* (*Trichomanes*), a series of such buds may be produced. (Occasional proliferation apices reported in *Trichomanes* sens. strict. and *Feea* may be of the same nature, but their ontogenetic origin is not known). It is significant also that in several of these genera, an apex in a definite position in the plant body which would ordinarily be expected to develop into a frond occasionally develops into a running stem (*Psilotum*, *Gonocormus*, and *Stromatopteris*). It is also of significance that in those genera which seem to produce incompletely appendicularized fronds, as evidenced by their terminal positions on recognizable branches or by the occurrence of a basal branch derived from the sister apex of the frond apex, generally express classical radial stem anatomy at least in part within their fronds.

The final stages in appendicularization as they exist within the extant Filicales might be illustrated as in Figure 26, which depicts diagrammatically several types of ontogenetic sequences in frond formation. The various sequences in each case begin with a stem apex with an apical cell with three cutting faces and exhibiting more or less symmetrical growth (A or H). (Please allow for the fact that certain filiform stems of the Hymenophyllaceae do not bear a single apical cell.) A lens-shaped apical cell represents both it and the linear prismatic series emanating from its two cutting faces or just a linear meristem in those cases where an apical cell is not present or not recognizable.

The end point, *i.e.* the most specialized state, in appendicularization (A and J) has been reached when the leaf meristem originates from a lens-shaped apical cell upon the dome of the stem apex. The primordium is thus bilateral and dorsiventral from its inception. This is apparently the condition which exists in most filiclean ferns insofar as is known.

Less specialized is the sequence illustrated by A, B, C, and G in which the leaf primordium at first shows an apical cell with 3 cutting faces and then shifts to one with two. This occurs in some species of *Actinostachys*, *Gleichenia*, and *Osmunda*. In the first two of these, the apical transformation occurs early in the life of the frond. In *Osmunda* it may be early or in one species not until just before the terminal pinna is formed.

Sequence A, B, C, D, E, and F represents an ontogenetic sequence of a still less appendicularized frond, *i.e.* more primitive. Two new apical cells both with 3 cutting faces are formed (B), one becomes lateral in position (C), it divides and two similar ones are formed (D) (this division plane is variable), one of these shifts over to the leaf type (far right in F). This type of sequence appears in *Stromatopteris*, at least two species of *Actinostachys*, at least two species of *Gleichenia*, and in several Hymenophyllaceae. In *Gonocormus* the divisions may be repeated in the formation of the "proliferations." Also, the morphological unit composed of the two apices on the right in F may occasionally develop directly from an individual apex of a long stem (*Stromatopteris* and some Hymenophyllaceae).

Series H and I (or A and I) represents the condition where the frond develops directly from the apex of a long stem. This occurs in *Psilotum*, although the apical cell remains triangular throughout the growth of the frond, and in *Tmesipteris* where the apex also remains radially symmetrical but only until just before the terminal pinna is formed. Also in *Psilotum*, the frond apex frequently leaves behind one to 10 small, apparently lateral apices near its base in a manner considered equivalent to the branching in D, E, and F.

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